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Estimating Effects of Permanent Environment, Lactation Stage, Age, and Pregnancy on Test-Day Yield

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ABSTRACT

Test-day variances for permanent environmental effects within and across parities were estimated along with lactation stage, age, and pregnancy effects for use with a test-day model. Data were test-day records for calvings since 1990 for Jerseys and for Holsteins from California, Pennsylvania, Texas, and Wisconsin. Single-trait repeatability models were fitted for milk, fat, and protein test-day yields. Method R and a preconditioned conjugate gradient equation solver were used for variance component estimation because of large data sets. Test-day yields were adjusted for environmental effects of calving age, calving season, and milking frequency and for estimated breeding value (EBV) expressed on a daily basis. To assess the effect of adjustments, test-day yields also were analyzed without adjustment. For adjusted data, permanent environmental variances across parities relative to phenotypic variance ranged from 8.3 to 15.2% for milk, 4.4 to 8.3% for fat, and 6.9 to 11.0% for protein across regions and breeds; relative permanent environmental variances within parity ranged from 31.4 to 34.7% for milk, 18.2 to 22.3% for fat, and 28.3 to 29.1% for protein and were similar across regions and breeds. Adjustment for EBV reduced permanent environmental variance across parities and removed cow genetic variance. Relative permanent environmental variances within parity from unadjusted test-day yields were nearly identical to those from adjusted test-day yields. For unadjusted test-day yields, heritabilities ranged from 0.19 to 0.30 for milk, 0.13 to 0.15 for fat, and 0.17 to 0.23 for protein. Adjustments for lactation stage, age at milking, previous days open, and days pregnant were estimated from adjusted test-day yields using the same single-trait repeatability models and variance ratios estimated for permanent environment

within and across parities. Those adjustments can be applied additively to test-day yields before evaluation analysis. Variance components and solutions for the various effects can be used to calculate test-day deviations in an analysis within herd that contributes to an analysis across herds.

(Key words: test-day model, genetic evaluation, yield traits)

Abbreviation key: PCG = preconditioned conjugate gradient

INTRODUCTION

Test-day models are being developed for national genetic evaluations of dairy cattle in many countries. Such models make better use of information that is collected on individual test days by accounting for environmental effects that are specific to that test day. This benefit can also be partly achieved by adjusting test-day yields for herd test-day effects before combining the yields into a lactation measure (Swalve, [2000](#)) that could be used in existing genetic evaluation systems (e.g., Wiggans, [1999](#)). This approach is used currently in New Zealand (Johnson, [1996](#)), Australia (Jones and Goddard, [1990](#)), and the northeastern US (Animal Breeding Group, [1999](#)). Such an approach could also be a step towards a full test-day model for US national evaluations. The large US cow population makes a full test-day model, such as the Canadian system described by Schaeffer et al. ([2000](#)), impractical computationally. Adjustment for test-day effects before analysis results in a simplified model that accounts only for environmental test-day effects. Several studies (Wiggans and Goddard, [1997](#); Gengler et al., [2000](#)) have suggested how a complete description of the (co)variance structure that includes effects of persistency and maturity across parities could be added to evaluation systems that are based on the simplified model so that large populations can be analyzed.

Test-day data are not available for all lactation records that currently are included in US evaluations, which makes a system that combines adjusted test-day and previous lactation records desirable. The multiplicative factors that are used for standardization of lactation records change record variances. To make the variance characteristics of adjusted test-day records similar to those for previous lactation records, the same multiplicative adjustments for age-season of calving and milking frequency (Karaca, [1997](#)) should be applied. After multiplicative adjustment, test-day yields could be additively adjusted for effects of lactation stage, age, and pregnancy and analyzed for test-day effects with a model that includes random nongenetic effects within and across parities. Finally, herd test-day solutions from that model could be used to adjust test-day records. After adjustment, test-day deviations could be combined into a lactation measure through best prediction (VanRaden, [1997](#)). Because precise estimates of herd test-day effects would be needed for such a model, other influences on test-day yield would have to be considered: calving age and season, lactation stage, herd, number of days open, and cow genetic and permanent environmental effects. Adjustment of test-day yields for lactation stage, age, and pregnancy effects prior to analysis is proposed to minimize computational requirements.

The purpose of this study was 1) to estimate test-day variance ratios for effect of permanent environment within and across parities in a single-trait repeatability model, 2) to estimate test-day effects of lactation stage, age, and pregnancy using the estimated variance ratios, and 3) to determine the impact of multiplicative adjustments before analysis by comparison with variance ratios and solutions based on unadjusted test-day yields.

MATERIALS AND METHODS

Data

Data were Holstein and Jersey lactation records that had been included in USDA (Beltsville, MD) national evaluations and were from calvings during 1990 and later. Holstein data were limited to herds from California, Pennsylvania, Texas, and Wisconsin; Jersey data represented the entire United States. Pennsylvania and Wisconsin were selected because of more complete reporting of test-day data; Texas was chosen for its geographical diversity, and California was considered to be an important dairy area. For computational convenience, Holstein data for estimates of variance ratios were grouped into subsets based on herd identification; herds were selected randomly without replacement. Each subset included approximately 5% of the entire data set for Pennsylvania, California, and Wisconsin and 53% of data from Texas. Record information included herd, animal identification, calving date, age, parity, test date, DIM, milking frequency, yields (milk, fat, and protein), previous days open, and days pregnant. Records for parities after fifth were excluded as is done for national evaluations. For each lactation, milk, fat, and protein yields from at least three test days were required as well as a test day before 90 DIM. Those requirements resulted in a mean number of parities per cow of slightly greater than two except for Wisconsin Holsteins, which averaged 1.9 parities per cow. Lactations included over eight test days per lactation except for Texas, which had 7.9 test days per lactation. Pedigree data were included for animals that were born after 1980.

Test-day yields were multiplied by factors used for standardization of lactation records for calving age, calving season, and milking frequency. For each cow, the EBV from the routine USDA evaluation was expressed on a daily basis (divided by 305) and subtracted from the standardized test-day yield to remove genetic influences and prevent genetic differences from biasing estimates of other effects. Test-day yields were not adjusted for previous days open as is done for lactation records, because this pregnancy effect was expected to differ by lactation stage. To assess the effect of multiplicative adjustments on test-day yield before evaluation analysis, different subsets of data for Holsteins and Jerseys were analyzed without multiplicative adjustments and EBV subtraction. Those subsets were chosen to contain approximately 1 million records. [Tables 1](#) and [2](#) show counts for adjusted and unadjusted data, respectively, for variance estimation of permanent environmental effects.

Table 1. Numbers of herds, cows, and test-day records for variance estimation of permanent environmental effects based on test-day yields that were adjusted for calving age, calving season, milking frequency, and EBV.

Breed	Region	Herds	Cows (no.)	Records
Holstein	California	67	58,292	1,038,395
	Pennsylvania	336	38,562	663,221
	Texas	246	68,626	1,112,418
	Wisconsin	460	53,540	861,404
Jersey	US	7767	471,987	7,686,268

Table 2. Numbers of herds, cows, animals, and test-day records for variance estimation for permanent environmental effects based on unadjusted test-day yields.

Breed	Region	Herds	Cows	Animals (no.)	Records
Holstein	California	74	64,643	103,769	1,095,927
	Pennsylvania	633	75,929	127,809	1,296,105
	Texas	268	68,685	109,106	1,135,903
	Wisconsin	471	50,747	85,860	824,461
Jersey	US	951	60,242	100,888	991,525

A separate random selection of herds was made for estimation of lactation stage, age, and pregnancy effects. The data sets for Holsteins included approximately 1 million test-day records per region.

Test-Day Models

A test-day model that partitions the effect of random permanent environment into components for effects across parities and within parity was used to describe test-day yields. Single-trait repeatability models were used; observations for successive parities of the same cow were assumed to be repeated observations of the same trait. The same models were applied to estimate variance components and to compute solutions.

For adjusted test-day yields, the model was

$$\mathbf{y} = \mathbf{X}_h \mathbf{h} + \mathbf{X}_a \mathbf{a} + \mathbf{X}_d \mathbf{d} + \mathbf{X}_s \mathbf{s} + \mathbf{X}_f \mathbf{f} + \mathbf{Z}_c \mathbf{c} + \mathbf{Z}_p \mathbf{p} + \mathbf{e}$$

where \mathbf{y} = vector of adjusted test-day yields; \mathbf{h} = vector of fixed effects of class of herd, test day, and milking frequency; \mathbf{a} = vector of fixed effects of age at milking (1-mo

classes) within parity (first, second, and later); \mathbf{d} = vector of fixed effects of DIM (10-d lactation-stage classes for DIM < 95 and 15-d lactation-stage classes for DIM \geq 95) within calving season (April through September and October through March) and parity; \mathbf{s} = vector of fixed effects of previous days open (10-d classes) within parity and 100-d lactation stage; \mathbf{f} = vector of fixed effects of days pregnant (10-d classes) within parity; \mathbf{c} = vector of random effects of permanent environment across parities with variance σ_c^2 ; \mathbf{p} = vector of random effects of permanent environment within parity with variance σ_p^2 ; \mathbf{e} = vector of random effects of residual with variance σ_e^2 ; \mathbf{X}_h , \mathbf{X}_a , \mathbf{X}_d , \mathbf{X}_s , \mathbf{X}_f , \mathbf{Z}_c , and \mathbf{Z}_p = incidence matrices that link \mathbf{y} and the respective vectors of fixed or random effects. The DIM were modelled in lactation-stage classes to avoid the imposition of a particular shape on the curve of solutions. Although test-day yields had been adjusted for calving age, calving season, and milking frequency prior to analysis because of their influence on yield variance, fixed effects for age at milking, calving season, and milking frequency also were included in the model to account for their additive effect on test-day yield.

The (co)variance matrix associated with \mathbf{c} and \mathbf{p} was

$$\text{Var} \begin{bmatrix} \mathbf{c} \\ \mathbf{p} \end{bmatrix} = \begin{bmatrix} \mathbf{I}\sigma_c^2 & 0 \\ 0 & \mathbf{I}\sigma_p^2 \end{bmatrix}$$

where \mathbf{I} = identity matrices of the order of the number of cows or parities. Permanent environmental covariance between adjusted test-day records of a cow was assumed to be σ_c^2 across parities and $\sigma_c^2 + \sigma_p^2$ for a given parity.

The correlation between records of an individual cow can be referred to as repeatability. Repeatability across parities (r_c) is the correlation between test-day records of a cow across parities; repeatability within parity (r_p) is the correlation between test-day records of a cow for a given parity. For adjusted test-day records, $r_c = \sigma_c^2 / (\sigma_c^2 + \sigma_p^2 + \sigma_e^2)$, and $r_p = (\sigma_c^2 + \sigma_p^2) / (\sigma_c^2 + \sigma_p^2 + \sigma_e^2)$.

For unadjusted test-day yields, an additive genetic effect \mathbf{g} with incidence matrix \mathbf{Z}_g and variance σ_g^2 was added to [Model 1](#) giving:

$$\mathbf{y} = \mathbf{X}_h\mathbf{h} + \mathbf{X}_a\mathbf{a} + \mathbf{X}_d\mathbf{d} + \mathbf{X}_s\mathbf{s} + \mathbf{X}_f\mathbf{f} + \mathbf{Z}_g\mathbf{g} + \mathbf{Z}_c\mathbf{c} + \mathbf{Z}_p\mathbf{p} + \mathbf{e}$$

where \mathbf{y} = vector of observed test-day yields. Nine genetic groups that each included 2 yr of birth were defined for unknown parents for births from 1980 through 1997. The vector \mathbf{g} includes only random additive genetic effects; consequently, nonadditive genetic cow effects are included in \mathbf{c} . For the adjusted analysis, no random additive genetic effect was included because EBV/305 had been subtracted from test-days yields to account for cow genetic effect.

The (co)variance structure of [Model 1](#) was extended to include \mathbf{g} :

$$\text{Var} \begin{bmatrix} \mathbf{g} \\ \mathbf{c} \\ \mathbf{p} \end{bmatrix} = \begin{bmatrix} \mathbf{A}\sigma_g^2 & 0 & 0 \\ 0 & \mathbf{I}\sigma_c^2 & 0 \\ 0 & 0 & \mathbf{I}\sigma_p^2 \end{bmatrix}$$

where \mathbf{A} = numerator relationship matrix. With \mathbf{g} included, permanent environmental covariance between unadjusted test-day records of a cow was assumed to be $\sigma_g^2 + \sigma_c^2$ across parities and $\sigma_g^2 + \sigma_c^2 + \sigma_p^2$ within parity. Then, for unadjusted records, $r_c = (\sigma_g^2 + \sigma_c^2) / (\sigma_g^2 + \sigma_c^2 + \sigma_p^2 + \sigma_e^2)$ = covariance between unadjusted test-day records of a cow across parities divided by total variance of adjusted records, and $r_p = (\sigma_g^2 + \sigma_c^2 + \sigma_p^2) / (\sigma_g^2 + \sigma_c^2 + \sigma_p^2 + \sigma_e^2)$ = covariance between unadjusted test-day records of a cow within parity divided by total variance. To allow comparison of repeatabilities between adjusted and unadjusted data, repeatabilities for unadjusted test-day yields also were computed as for adjusted test-day yields without σ_g^2 included.

Variance Components

A practical difficulty of test-day models is the extensive computational requirement that results from the large increase in unknowns to be solved. Large mixed-model equation systems can be solved only by powerful iterative methods. Although the test-day repeatability model represents the least complex of test-day models, estimation of variance components from most or all of the data set was a major challenge. To address this problem, Method R (Reverter et al., [1994](#)) and a preconditioned conjugate gradient (PCG) algorithm to solve equations (Strandén and Lidauer, [1999](#)) were implemented to estimate variance ratios for random permanent environmental effects within and across parities and for the additive genetic effect for unadjusted test-day yields. The procedure developed by Druet et al. ([2001](#)), which was based on the Method R programs of Misztal ([1997](#)), was used. Method R is able to accommodate large data sets because the procedure is based on repeated solutions of standard mixed-model equations. Misztal et al. ([1997](#)) estimated parameters for populations as large as 4 million animals with Method R procedures. In this study, the largest data set to which Method R was applied included 7,686,268 test-day records from 471,987 Jersey cows.

Iterations from Method R were assumed to have converged when regression factors ranged from 0.9998 to 1.0002. Method R and PCG solvers (used as a combined algorithm) were applied 6 times to breed-region data. For each application, a different randomly selected subset (50%) of the complete breed-region data was used. Variance ratios were averaged across the six samples.

Lactation Stage, Age, and Pregnancy Effects

Estimates of effects of lactation stage (10-d lactation-stage classes for DIM < 95 and 15-d lactation-stage classes for DIM \geq 95), age at milking (1-mo classes from 20 to 96 mo), previous days open (10-d classes), and days pregnant (10-d classes) were calculated for use as additive corrections to test-day milk, fat, and protein yields. Separate effects were estimated for the four regions for Holsteins. Single-trait repeatability models similar to Models [1](#) and [2](#) were used to estimate fixed effects simultaneously with the addition of a fixed effect for previous days open. Because the fixed environmental effects vary with parity, all were calculated separately for first, second, and later parities except for previous days open, which by definition (the days not pregnant during the previous lactation) was limited to second and later parities. For estimation of lactation-stage effects, two calving seasons were defined within parity: April through September and October through March. Age at milking was limited to 20 to 45 mo for first parity, 32 to 55 mo for second parity, and 45 to 96 mo for later parities. Because fewer days open during previous lactation may depress yield during current lactation, three lactation stages (<100, 100 through 199, and >199 d) were defined to estimate the effect of previous days open. Previously estimated variance ratios for random effects were used in the estimation of fixed effects. Solutions for lactation stage, age at milking, previous days open, and days pregnant were smoothed by fitting segmented quadratic polynomials (Fuller, [1969](#)). Adequate fit was achieved by defining up to two join points, which were selected based on visual appraisal of curves.

RESULTS AND DISCUSSION

Variance Components

Mean number of rounds of iteration required to achieve convergence for estimation of variance components generally ranged from 300 to 1300. Because of the inclusion of a random animal effect, more rounds (700 to 2000) of iteration were required for convergence for [Model 2](#) than for [Model 1](#).

Mean variance estimates for random effects were expressed as percentages of phenotypic variance for adjusted ([Table 3](#)) and unadjusted ([Table 4](#)) test-day yields. For adjusted test-day yields, additive genetic variance was not included in total variance because EBV had already been subtracted.

Table 3. Mean variance of random effects relative to phenotypic variance and approximate standard errors from test-day yields that were adjusted for calving age, calving season, milking frequency, and EBV ([Model 1](#)).

Yield trait	Breed	Region	Permanent environmental variance				Residual variance		
			Across parities	Within parity					
			Mean	SEM	Mean	SEM	Mean	SEM	
			(%)						
Milk	Holstein	California	12.1	0.91	31.8	0.60	56.2	0.39	
		Pennsylvania	11.6	0.87	32.8	0.86	55.6	0.31	
		Texas	8.3	0.27	34.7	0.51	56.9	0.26	
		Wisconsin	11.6	0.19	33.2	0.26	55.3	0.29	
Fat	Jersey	US	15.2	0.45	31.4	0.34	53.4	0.18	
	Holstein	California	6.3	0.30	19.1	0.29	74.6	0.24	
		Pennsylvania	8.3	0.43	19.9	0.30	71.8	0.36	
		Texas	4.4	0.27	18.2	0.32	77.4	0.12	
		Wisconsin	7.8	0.53	21.0	0.53	71.2	0.32	
	Jersey	US	7.0	0.16	22.3	0.09	70.7	0.10	
	Protein	Holstein	California	8.6	0.33	27.3	0.31	64.1	0.46
			Pennsylvania	9.7	0.52	28.5	0.46	61.7	0.36
Texas			6.9	0.23	28.3	0.13	64.8	0.31	
Wisconsin			9.1	0.52	29.1	0.59	61.8	0.66	
Jersey		US	11.0	0.09	28.8	0.12	60.2	0.09	

Table 4. Mean variance of random effects relative to phenotypic variance and approximate standard errors from test-day yields that were not adjusted for calving age, calving season, milking frequency, and EBV ([Model 2](#)).

			Permanent environmental variance								
Yield trait	Breed	Region	Genetic variance		Across parities		Within parity		Residual variance		
			Mean	SEM	Mean	SEM	Mean	SEM	Mean	SEM	
(%)											
Milk	Holstein	California	17.7	1.57	14.5	1.35	23.8	0.46	44.0	0.77	
		Pennsylvania	19.4	1.38	12.8	1.04	26.0	0.50	41.8	0.60	
		Texas	21.3	1.69	13.0	1.37	25.1	0.32	40.5	0.61	
		Wisconsin	16.7	1.98	15.8	1.13	26.3	0.38	41.2	0.83	
Fat	Jersey	US	30.2	1.44	11.2	1.09	20.4	0.51	38.2	0.39	
	Holstein	California	12.4	0.45	9.7	0.29	14.7	0.17	63.2	0.23	
		Pennsylvania	14.9	0.94	9.5	0.48	16.5	0.27	59.1	0.36	
		Texas	11.0	0.51	8.4	0.65	15.3	0.18	65.2	0.13	
		Wisconsin	14.3	0.98	10.6	0.87	16.8	0.28	58.2	0.23	
	Jersey	US	14.8	1.65	9.7	1.15	17.0	0.29	58.5	0.37	
	Protein	Holstein	California	17.6	2.55	10.4	2.20	21.4	0.46	50.7	0.75
			Pennsylvania	18.0	1.89	13.1	1.51	22.2	0.17	46.7	0.31
Texas			16.0	0.71	11.9	1.00	22.0	0.23	50.2	0.50	
Wisconsin			15.9	1.03	14.9	0.72	22.6	0.28	46.6	0.59	
Jersey	US	22.7	2.02	11.5	1.45	20.2	0.11	45.6	0.70		

Regardless of adjustment of test-day yields, permanent environmental variances were consistently higher within parity than across parities for all traits, regions, and breeds. However, trait, region, and breed differences were evident. For adjusted test-day yields ([Table 3](#)), mean permanent environmental variances across parities were 10.9% for Holsteins (15.2% for Jerseys) for milk, 6.7% (7.0%) for fat, and 8.6% (9.8%) for protein; variances within parity were 33.1% for Holsteins (31.4% for Jerseys) for milk, 19.6% (22.3%) for fat, and 28.3% (28.8%) for protein. Corresponding variances for unadjusted test-day yields ([Table 4](#)) were 14.0% for Holsteins (11.2% for Jerseys) for milk, 9.6% (9.7%) for fat, and 12.6% (11.5%) for protein across parities and 25.3% (20.4%) for milk, 15.8% (17.0%) for fat, and 22.0% (20.2%) for protein within parity. Mean residual variances were 56.0% for Holsteins (53.4% for Jerseys) for milk, 73.8% (71.2%) for fat, and 63.1% (60.2%) for protein for adjusted test-day yields and 41.9% (38.2%) for milk, 61.4% (58.5%) for fat, and 48.6% (45.6%) for protein for unadjusted test-day yields.

For adjusted Holstein test-day yields ([Table 3](#)), permanent environmental variances were consistently lowest for Texas for all yield traits, which resulted in increased residual variances. Because of this result, a second random sampling for Texas was conducted, and variance estimates were found to be consistent with those from the first random

subset. Sampling variance was in an acceptable range as shown by the relatively low standard errors for the means. Permanent environmental variances of unadjusted Holstein test-day yields ([Table 4](#)) were similar for all regions, which suggests that the regional differences for adjusted Holstein test-day yields were caused by the adjustment factors used.

Method R provides estimates of variance ratios that can be converted to variances that are expressed as a percentage of phenotypic variance rather than actual variances. Therefore, variances could be made comparable across models to show the sensitivity of analysis to multiplicative data adjustment prior to analysis and EBV subtraction ([Table 5](#)) by increasing the total variance from adjusted test-day yields ([Model 1](#)) by the additive genetic variance from unadjusted test-day yields [Model 2](#). Although such variances are rough approximations, no other suitable method was found to allow easy comparison of models. Subtraction of EBV from adjusted test-day yields that were used with [Model 1](#) was assumed to have reduced total phenotypic variance by the same amount of variance as the additive genetic variance that was estimated with the unadjusted test-day yields and [Model 2](#).

TABLE 5. Variance of random effects for data that were adjusted for calving age, calving season, milking frequency, and EBV ([Model 1](#)), relative to phenotypic variance that included additive genetic variance from unadjusted data ([Model 2](#)).

Yield trait	Breed	Region	Genetic variance	Permanent environmental variance		Residual variance	
				Across parities	Within parity		
				(%)			
Milk	Holstein	California	18.4	9.8	25.9	45.9	
		Pennsylvania	20.4	9.2	26.1	44.3	
		Texas	23.0	6.4	26.8	43.7	
		Wisconsin	18.1	9.5	27.1	45.3	
Fat	Jersey	US	29.6	10.7	22.1	37.6	
	Holstein	California	12.8	5.5	16.7	65.1	
		Pennsylvania	16.8	7.0	15.3	60.8	
		Texas	11.5	3.9	16.1	68.4	
		Wisconsin	14.8	6.6	17.9	60.7	
	Jersey	US	15.0	6.0	18.9	60.0	
	Protein	Holstein	California	17.9	7.0	22.4	52.7
			Pennsylvania	19.1	7.8	23.1	50.0
Texas			17.1	5.7	23.5	53.8	
Wisconsin			17.3	7.5	24.0	51.2	
Jersey	US	23.0	8.5	22.2	46.4		

When relative variances for adjusted ([Model 1](#)) and unadjusted ([Model 2](#)) data were made comparable, permanent environmental variance across parities generally was much lower for adjusted ([Table 5](#)) than for unadjusted ([Table 4](#)) data regardless of yield trait, breed, or region. Those decreases were reflected by slight increases in permanent environmental variance within parity, genetic variance, and residual variance. Multiplicative adjustment of data for calving age, calving season, and milking frequency and EBV subtraction before analysis reduced permanent environmental variance across parities. For unadjusted data, effects of calving age, calving season, and milking frequency may be partially confounded with effect of permanent environment across parities.

Ratios of residual variance to variances for other random effects were calculated from relative variances for adjusted ([Table 1](#)) and unadjusted ([Table 2](#)) data. Variance ratios for milk yield are shown in [Table 6](#). For permanent environment within parity, variance ratios were remarkably similar across breeds and regions for adjusted data: 1.6 to 1.8 for milk yield, 3.3 to 4.2 for fat yield (not shown in table), and 2.1 to 2.4 for protein yield

(not shown in table). Variance ratios for permanent environment across parities ranged from 3.5 to 6.8 for milk, 8.6 to 17.6 for fat, and 5.5 to 9.4 for protein for adjusted data. Although ratios for permanent environment within parity were similar regardless of data adjustment, ratios for permanent environment across parities were smaller for unadjusted than for adjusted data as expected from the estimated relative variances in [Table 5](#).

TABLE 6. Ratios of residual variance to variances for other random effects on milk yield and approximate standard errors for data that were adjusted for calving age, calving season, milking frequency, and EBV ([Model 1](#)) and unadjusted data ([Model 2](#)).

		Adjusted data (Table 1)				Unadjusted data (Table 2)					
		Permanent environmental variance				Permanent environmental variance					
		Across parities		Within parity		Genetic variance		Across parities		Within parity	
Breed	Region	Ratio	SE	Ratio	SE	Ratio	SE	Ratio	SE	Ratio	SE
Holstein	California	4.7	0.37	1.8	0.03	2.5	0.25	3.0	0.28	1.8	0.02
	Pennsylvania	4.8	0.35	1.7	0.05	2.2	0.18	3.3	0.24	1.6	0.04
	Texas	6.8	0.19	1.6	0.03	2.5	0.36	2.6	0.17	1.6	0.02
	Wisconsin	4.8	0.09	1.7	0.02	2.3	0.28	3.0	0.28	1.7	0.13
Jersey	US	3.5	0.11	1.7	0.02	1.3	0.07	3.4	0.29	1.9	0.05

Repeatabilities for effects of permanent environment ([Table 7](#)) for adjusted test-day yields ranged across yield traits and breeds from 7 to 15% across parities and from 26 to 47% within parity; for unadjusted test-day yields, repeatabilities ranged from 23 to 41% across parities and from 38 to 62% within parity. In a study of Belgian test-day data, Coenraets ([1994](#)) used a similar model with unadjusted test-day yields and reported repeatabilities of 37 to 40% across parities and 59% to 67% within parity.

Table 7. Repeatabilities for permanent environment across parities (r_c) and within parity (r_p) and heritabilities (h^2).

Data	Breed	Milk			Fat			Protein		
		r _c	r _p	h ²	r _c	r _p	h ²	r _c	r _p	h ²
		(%)								
Adjusted test-day yield ¹	Holstein	11	44	...	7	26	...	9	37	...
	Jersey	15	47	...	7	29	...	11	40	...
Unadjusted test-day yield ²	Holstein	33	58	19	23	38	13	29	51	17
	Jersey	41	62	30	24	41	15	34	54	23
Unadjusted test-day yield with genetic variance excluded ³	Holstein	17	48	...	11	29	...	15	41	...
	Jersey	16	45	...	11	31	...	15	41	...

¹Repeatabilities computed from variances in [Table 3](#) for test-day yields that were adjusted for calving age, calving season, milking frequency, and EBV.

²Repeatabilities and h^2 computed from variances in [Table 4](#) for unadjusted test-day yields.

³Repeatabilities computed from variances in [Table 4](#) for unadjusted test-day yields but with genetic variance excluded.

[Table 7](#) also includes repeatabilities for effects of permanent environment from unadjusted test-day yields but with genetic variance excluded so that the repeatabilities could be compared with those for adjusted test-day yields. As expected from the estimated relative variances in [Table 5](#), only r_c tended to be larger when genetic variance was excluded from unadjusted data; r_p were nearly identical regardless of data adjustment. When genetic variance was excluded from the repeatabilities reported by Coenraets (1994) for Belgian test-day data, repeatabilities for effect of permanent environment ranged from 20 to 22% across parities and from 48 to 58% within parity.

Heritabilities computed from unadjusted data ([Table 7](#)) were higher for Jerseys than for Holsteins for all yield traits, which was consistent with the results of Lofgren et al. (1985). A possible explanation for the higher heritabilities for Jerseys is the larger percentage of registered cattle (Norman and Powell, 1983) compared with the Holstein population, which would result in more accurate and complete animal identification. Heritabilities for fat yield were lower (13% for Holsteins and 15% for Jerseys) than for milk (19 and 30%, respectively) and protein (17 and 23%) yields. Conraets (1994) estimated similar heritabilities (21 to 23%) with Belgian test-day data and a similar model.

Lactation Stage, Age, and Pregnancy Effects

Lactation stage. Join points for curves that were fit to solutions for adjusted test-day yields were at 40 and 70 DIM for all yield traits, parities, breeds, and regions. For adjusted test-day milk yield of Wisconsin Holsteins ([Figure 1](#)), the greatest difference in

lactation-stage effects due to calving season occurred at peak yield (30 to 70 DIM). First-parity curves peaked lower but were more persistent than curves for second and later parities. The greater persistency for first-parity cows likely resulted from lower peak yields and from growth maturation during first lactation.

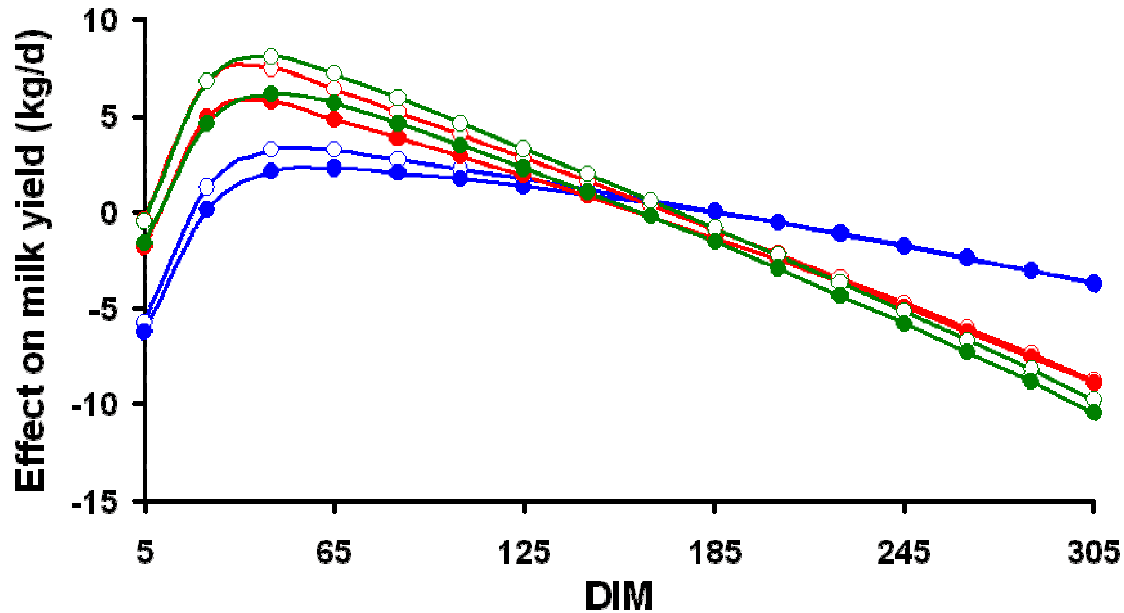


Figure 1. Effect of lactation stage (DIM) on Wisconsin Holstein test-day milk yield adjusted for calving age, calving season, milking frequency, and EBV by parity (1 = first, 2 = second, and 3 = third and later) and calving season (1 = April through September and 2 = October through March): parity 1, season 1 (—●—); parity 1, season 2 (---○---); parity 2, season 1 (—●—); parity 2, season 2 (---○---); parity 3, season 1 (—●—); and parity 3, season 2 (---○---).

Curves for effect of lactation stage on adjusted test-day fat yield of Wisconsin Holsteins ([Figure 2](#)) were quite flat for first parity with only a slight decrease over the entire lactation. A steeper slope was observed for second and later parities. For later parities, lactation-stage effect on fat yield declined by 0.74 kg from 5 to 305 d for calvings during October through March. For calvings during April through September, the corresponding decline was 0.65 kg.

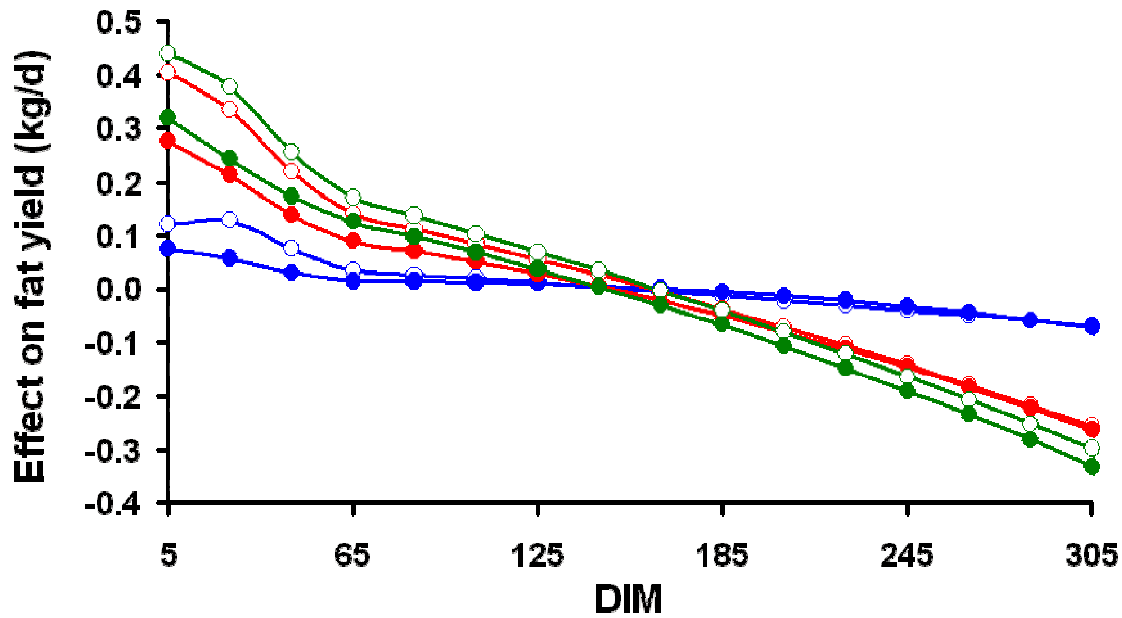


Figure 2. Effect of lactation stage (DIM) on Wisconsin Holstein test-day fat yield adjusted for calving age, calving season, milking frequency, and EBV by parity (1 = first, 2 = second, and 3 = third and later) and calving season (1 = April through September and 2 = October through March): parity 1, season 1 (—●—); parity 1, season 2 (---○---); parity 2, season 1 (—●—); parity 2, season 2 (---○---); parity 3, season 1 (—●—); and parity 3, season 2 (---○---).

For effect of lactation stage on adjusted test-day protein yield of Wisconsin Holsteins ([Figure 3](#)), the curves for first parity were quite different from those for second and later parities. First-parity curves had a slight peak near midlactation; for second and later parities, effect of lactation stage declined over the entire lactation. For both fat ([Figure 2](#)) and protein ([Figure 3](#)), the lactation-stage effect on adjusted test-day yields due to calving season was similar to that for milk yield.

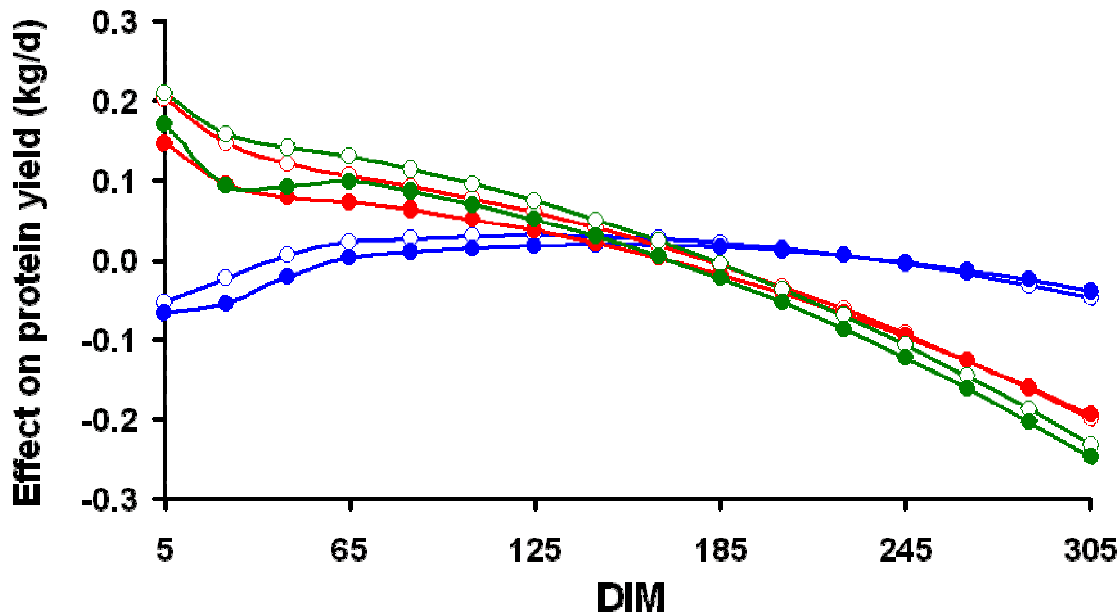


Figure 3. Effect of lactation stage (DIM) on Wisconsin Holstein test-day protein yield adjusted for calving age, calving season, milking frequency, and EBV by parity (1 = first, 2 = second, and 3 = third and later) and calving season (1 = April through September and 2 = October through March): parity 1, season 1 (—●—); parity 1, season 2 (---○---); parity 2, season 1 (—●—); parity 2, season 2 (---○---); parity 3, season 1 (—●—); and parity 3, season 2 (---○---).

Curves for lactation-stage effect were similar for all Holstein regions for all traits. The corresponding curves were similarly shaped for Jersey yield traits, but the magnitude of the effect was slightly less for milk yield.

Age at milking. Join points were at 28 and 36 mo of age at milking for first parity and at 34 and 40 mo for second parity; no join points were assigned for later parities. Effects of age at milking on test-day milk yields of first-lactation Holsteins ([Figure 4](#)) were compared for adjusted and unadjusted data. With unadjusted data, effects on test-day yield from age at milking increase with age as expected, and curves were similar for all regions. For adjusted data, the effect declined somewhat with age but was still similar among regions. This decline may have resulted from the application of the multiplicative age adjustments and the confounding of age at milking with lactation stage. High yields during early lactation are affected more than lower yields during later stages of lactation by the same multiplicative factor. The shape of the age curve is, therefore, an artifact of the multiplicative adjustment of data before analysis. However, including age at milking in the model still is useful in improving the accuracy of estimates of other effects. The first-parity curves for effect of age at milking on Jersey test-day yield were similar to those for Holsteins. For later parities, the effect of age at milking was less, but differences were greater among regions and between breeds.

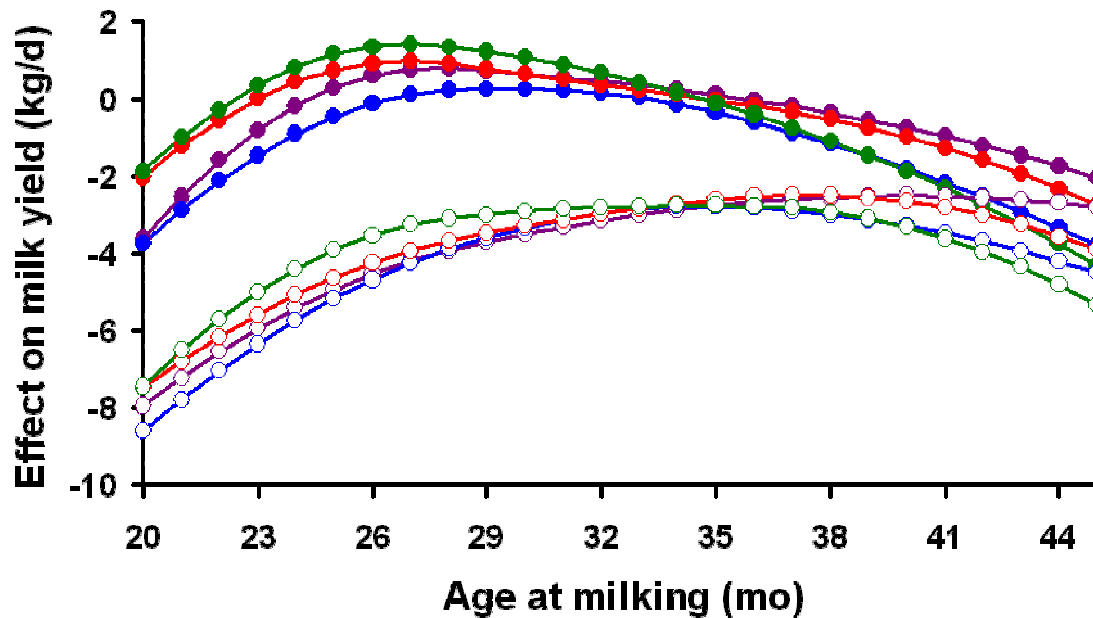


Figure 4. Effect of age at milking on test-day milk yield of first-lactation Holsteins based on data adjusted for calving age, calving season, milking frequency, and EBV from California (—●—), Pennsylvania (—●—), Texas (—●—), and Wisconsin (—●—) and unadjusted data from California (---○---), Pennsylvania (---○---), Texas (---○---), and Wisconsin (---○---).

Previous days open. No join points were assigned for previous days open. Long days open during previous parities affected test-day milk and component yields positively. For Wisconsin Holsteins, the effect of previous days open on adjusted test-day milk yield ([Figure 5](#)) was greater for later stages of lactation than for earlier stages. Similar curves were found for adjusted test-day fat and protein yields. As expected, short calving intervals (conception at <65 d postpartum) reduced yield in the next lactation regardless of lactation stage. Difference between effects for 60 and 240 d open on Holstein adjusted test-day yield across regions, parities, and lactation stages ranged from -2.71 to 0.05 kg for milk, from -0.10 to -0.03 kg for fat, and from -0.08 to 0.03 kg for protein. Effects of previous days open on adjusted test-day yields were similar for Jerseys.

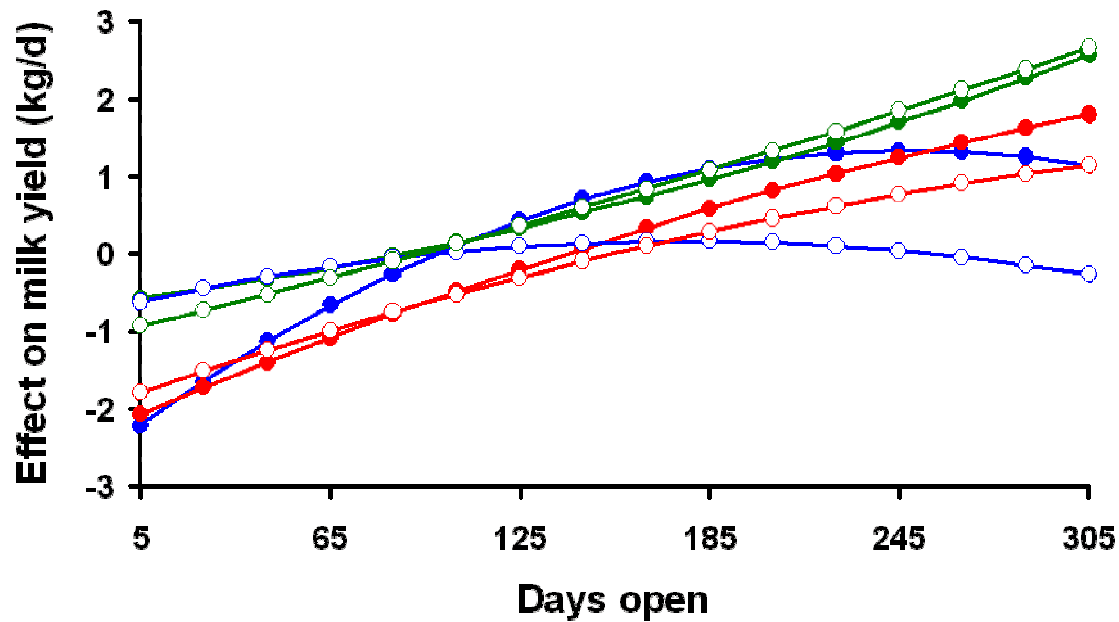


Figure 5. Effect of previous days open on Wisconsin Holstein test-day milk yield adjusted for calving age, calving season, milking frequency, and EBV by parity (2 = second and 3 = third and later) and lactation stage (1 = DIM < 100, 2 = DIM of 100 through 199, and 3 = DIM > 199): parity 2, stage 1 (—●—); parity 2, stage 2 (—●—); parity 2, stage 3 (—●—); parity 3, stage 1 (—○—); parity 3, stage 2 (—○—); and parity 3, stage 3 (—○—).

Days pregnant. One join point was defined at 150 d pregnant. Regardless of yield trait, pregnancy depressed yield, particularly during the last third of lactation. For milk yield of cows 240 d pregnant compared with open cows, effect on adjusted test-day yield ranged from -6.09 kg (Wisconsin) to -4.62 kg (Texas) for first parity, from -5.64 kg (Wisconsin) to -3.88 kg (Texas) for second parity, and from -5.63 to -3.98 kg (Texas) for later parities. For fat yield, the corresponding effect ranged from -0.16 kg (Wisconsin) to -0.11 kg (Texas) for first parity, from -0.19 kg (Wisconsin) to -0.10 kg (Texas) for second parity, and from -0.16 kg (Wisconsin) to -0.11 kg (Texas) for later parities. Similar ranges were found for protein. Pregnancy effects for adjusted test-day yield of first-lactation Wisconsin Holsteins (Figure 6) were similar to those for Holsteins in other regions, and curves were similarly shaped for second and later parities. Effect of days pregnant on adjusted test-day yield was slightly less for Jerseys.

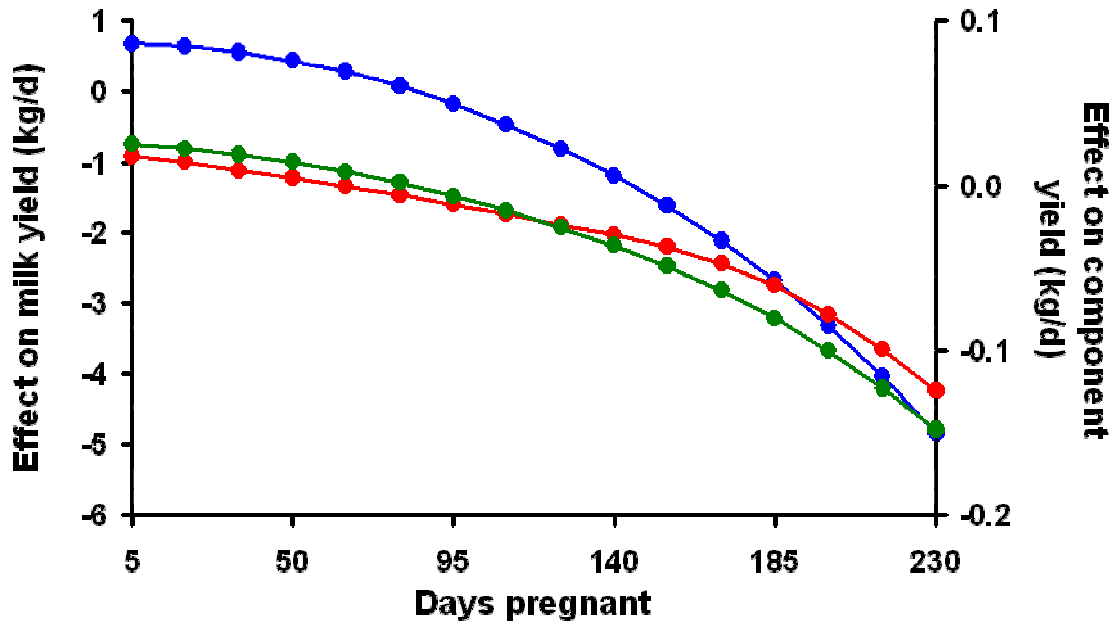


Figure 6. Effect of days pregnant on test-day milk (—◆—), fat (—■—), and protein (—●—) yields of first-lactation Wisconsin Holsteins based on data adjusted for calving age, calving season, milking frequency, and EBV by yield traits.

CONCLUSIONS

Estimation of variance components is a crucial step in the implementation of a genetic evaluation system based on test-day yields. Prediction of breeding values relies on knowledge of variance components. In this study, Method R and PCG were effective for variance component estimation based on extremely large data sets such as the US dairy cattle population. Heritabilities, variance components, and additive adjustments estimated in this study could be used to calculate test-day deviations in an analysis within herd that contributes to an analysis across herds as part of a genetic evaluation system that is based on a test-day model.

Solutions for effects of age at milking, lactation stage, previous days open, and days pregnant on adjusted test-day milk and component yields and SCS were calculated for all breeds that currently are genetically evaluated by USDA. Coefficients for equations that represent those solutions are [available](#) from the Animal Improvement Programs Laboratory.

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